Anopheles (Anopheles) pseudopunctipennis Theobald (Diptera: Culicidae): Neotype Designation and Description

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ABSTRACT Detailed morphological descriptions and illustrations are provided for the adult male and female, male genitalia, pupal, and larval stages of *Anopheles* (*Anopheles*) *pseudopunctipennis* Theobald, a major vector of human malaria in Central and South America. Taxonomic and related literature records, diagnostic features, distribution, and bionomics of the species are included. A neotype male for the species from the type locality of Grenada is designated.

KEY WORDS *Anopheles pseudopunctipennis*, neotype, description, mosquitoes, malaria

Anopheles (Anopheles) pseudopunctipennis Theobald is considered a major vector of human malaria in Central and South America, particularly in Mexico, Guatemala, Nicaragua, Bolivia, Ecuador, Peru, and Argentina (Pan American Health Organization 1994). It is widely distributed in the New World (Rozeboom 1941). It is found from the southern United States (40° N) to the northern part of Argentina (30° S) along the Andes, with eastern extension into Venezuela and the Lesser Antilles (Manguin et al. 1996). It is the most important malaria vector in the foothills of mountainous areas and other elevated (up to 2800 m), rugged malaria-endemic areas of North, Central, and South America (Aitken 1945, Rodriguez and Loyola 1989, Gorham et al. 1973).

Anopheles pseudopunctipennis was first described by Theobald (1901: 305–306) from one male and one female from Grenada (Dr. Hatton, per Dr. Daniels), mounted in balsam. However, these two specimens, as in the case of other Daniels material, are presumably lost or nonextant. The original adult description (Theobald 1901) was incomplete for accurate identification of the species, and no detailed descriptions of the larval and pupal stages, or of the male terminalia have been made from the type locality (Grenada). In view of this, it becomes imperative to provide detailed descriptions of various life stages and to designate a neotype for this important species.

From 1944–1950, five subspecies and one variant of *An. pseudopunctipennis* were morphologically described from different areas of South America, including Ecuador, Colombia, Chile, and Argentina. Three names that were applied to this species between 1907–1912 are currently in synonymy.

In the present paper, descriptions and illustrations are provided for the adult female and male, pupa, and larva of this species from the type locality. A male neotype from the type locality is also designated.

Materials and Methods

Except for wing spot nomenclature, which is taken from Wilkerson and Peyton (1990), the terminology and abbreviations of Harbach and Knight (1980, 1982) are used in the morphological characters and illustrations. Acronyms of type depositories are as follows: Division de Malariologia/Instituto Nacional Para Programas Especiales de Salud, Bogota, Colombia (DMB), Instituto Biologie "Juan Noe," Santiago, Chile (IZC), Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN). Abbreviations used are as follows: E, egg; F, female; G, genitalia; L, larva; Le, larval exuviae; LU, location unknown; M, male; NE, type nonexistent; P, pupa; Pe, pupal exuviae; ssp., subspecies; var., variety. An asterisk following the abbreviation of a given life stage indicates that part of the life stage was illustrated in the publication cited. Collection codes of the most recent collections consist of a country code in capital letters followed by a collection number (e.g., GR-33-1 is an individual from collection 33 from Grenada) (specimen numbers 1–99 are used if there are associated larval and pupal exuviae, numbers 100 and up are used

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if there is only a pupal exuviae). Progeny from a single female are indicated by a number in parentheses, e.g., GR 33(5)-1 is an individual from female number 5.

Taxonomic Treatment

Anopheles (Anopheles) pseudopunctipennis Theobald (Figs. 1–3)

Anopheles pseudopunctipennis Theobald 1901: 305 (M, F). Type: Grenada (NE); Howard et al. 1917: 1020 (M*, F*, L*); Aitken 1945: 327 (M, F*, P*, L, E*, taxonomy, biology); Vargas and Martinez Palacios 1956: 83 (M*, F*, P*, L*).

Anopheles peruvianus Tamayo 1907. *In* Tamayo and Garcia 1907: 35 (M*, F*, P*, L*). Type: Huacachina, San Pedro de Lloc, Lima, Verano, Otono, Chanchmayo, Peru (NE); Lane 1953: 160 (listed as synonym).

Proterorhynchus argentinus Brethes 1912: 15 (M, F). Type: North Tucuman, Salta, Jujuy, Santiago del Estero, Argentina (MACN); Howard et al. 1917: 1015 (listed as synonym); Casal, *in* Belkin, Schick and Heinemann 1968: nine (lectotype desig.).

Anopheles tucumanus Lahille 1912: 253 (F*). Type: Rio Sali, Argentina (NE); Howard et al. 1917: 1015 (listed as synonym).

Anopheles (Anopheles) pseudopunctipennis ssp. *pseudopunctipennis* Theobald, Levi-Castillo 1944: 1 (M*, E*); Aitken 1945: 344; Carpenter, Middlekauff and Chamberlain 1946: 66 (M*, F*, L*); Freeborn, *in* Boyd 1949: 391; Lane 1953: 160 (M*, F*, P*, L*, E*); Carpenter and LaCasse 1955: 46 (M* F*, L*).

Anopheles (Anopheles) pseudopunctipennis ssp. *levicastilloi* Levi-Castillo 1944: 1 (M*, E*; as variety). Type: Guayasa, Ecuador (LU); Levi-Castillo 1945: 41 (M*, F, P, L*, E*; to ssp. status); Lane 1953: 160 (possible synonymy with *An. (Ano.) pseudopunctipennis* ssp. *psuedopunctipennis*).

Anopheles (Anopheles) pseudopunctipennis ssp. *rivadeneirai* Levi-Castillo 1945: 33 (M*, F*, L*, E*). Type: Provs. of Carchi, Imbabura, Pichincha, Cotopaxi, Tungurahua, Chimborazo, Canar, Azuay and Loja; Interandian Region, Ecuador (LU); Lane 1953: 160 (possible syn. with *An. (Ano.) pseudopunctipennis* ssp. *psuedopunctipennis*).

Anopheles (Anopheles) pseudopunctipennis ssp. *pattersoni* Alvarado and Heredia 1947: 73 (E*; as var.). Type: Tucuman, Argentina (NE); Lane 1953: 161 (to ssp. status).

Anopheles (Anopheles) pseudopunctipennis var. *bifoliata* Qsorno-Mesa and Munoz-Sarmiento 1948: 105 (M*, L*, E*). Type: Florida, Valle del Cauca, Colombia (DMB).

Anopheles (Anopheles) pseudopunctipennis ssp. *neghmei* Mann 1950: 34 (M, F*, L*, E*). Type: Ouebrada de Minemine, Tarapaca, Chile (IZC).

Anopheles (Anopheles) pseudopunctipennis ssp. *noei* Mann 1950: 37 (M, F, L*, E*). TYPE: Oasis de Suca, Tarapaca, Chile (IZC).

Other Literature Records. Shannon and Davis 1927: 662–678 (notes on biology, Argentina); Shannon 1930: 442–447 (larval habitats, Peru); Hoffmann 1931: 523–529 (larval habitats, Mexico); Hoffmann and Samano 1938: 182–192 (larval habitats, Mexico); Root and Andrews 1938: 565–578 (larval habitats, Grenada); Simmons 1941: 113–130 (as malaria vector, Central and South America); Rodriguez and Loyola 1989: 15–40 (as malaria vector in mountainous areas, Mexico); Savage et al. 1990: 612–619 (larval habitats, Mexico); Rejmankova et al. 1991: 827–839 (larval habitats, Mexico), Rejmankova et al. 1993: 979–991 (larval habitats, Belize); Estrada-Franco et al. 1992: 297–299 (cross breeding, electrophoretic analysis); Estrada-Franco et al. 1993a: 735–745 (enzyme electrophoresis, Mexico, Peru, Bolivia); Estrada-Franco et al. 1993b: 746–755 (cross breeding, Mexico, Peru, Bolivia); Fernandez-Salas et al. 1994 (larval habitats, Mexico); Manguin et al. 1993: 405–406 (larval habitats and abundance, Grenada); Manguin et al. 1995: 362–377 (electrophoretic survey, population genetics, North, Central and South America); Manguin et al. 1996: 620–625 (larval habitats, North, Central and South America); Bond-Compean et al. 1998: 220 (larval habitat, Mexico); Coetzee et al. 1999: 650–652 (cross breeding, cytogenetics, Mexico, Grenada).

Original Description

In support of previous and present interpretations of the name *pseudopunctipennis*, the original description given by F. V. Theobald (1901) is as follows. "Wings much as in *An. punctipennis* Say, but the fringe with yellow spots. Legs long, unbanded, brown, pale at the base. Fore ungues of male unequal, mid and hind equal and simple. *Female.* Antenna brown, basal joint testaceous, base of the second joint pale, and also a small pale band at the base of all the following joints; proboscis dark brown, labela yellowish; palpi dark brown, densely scaled at the base, apex yellow, and also two narrow yellow bands below, slightly hairy, hairs black, except at the apex, where they are yellow; clypeus dark brown. Thorax yellowish-brown (denuded), with a dark patch on each side of the mesonotum behind; metanotum dark brown; pleurae yellowish brown, with darker brown patches. Abdomen brown, the segments paler at the base; hairy. Legs deep brown, coxae, trochanters, and base of femora pallid; knee spot pale; ungues equal and simple. Halteres with pale stem and fuscous knob. Wings with two yellowish-white spots on the upper costal border, rest of the edge black, rather densely scaled; first submarginal cell longer and narrower than second posterior cell, its stem nearly as long as the cell; mid cross-vein a little nearer the base of the wing than supernumerary cross-vein; posterior cross-vein still nearer the base of the wing; scales of the wings disposed as follows: First long vein with three distinct large white spots, one at the base, one underneath the large costal spot, and one between; second long vein with a dark patch near its base, all the lower branch of the fork-cell dark, and most of the upper; third long vein mostly yellowish-white, with two black patches, one toward the base, the other toward the tip; fourth long vein mostly pale,

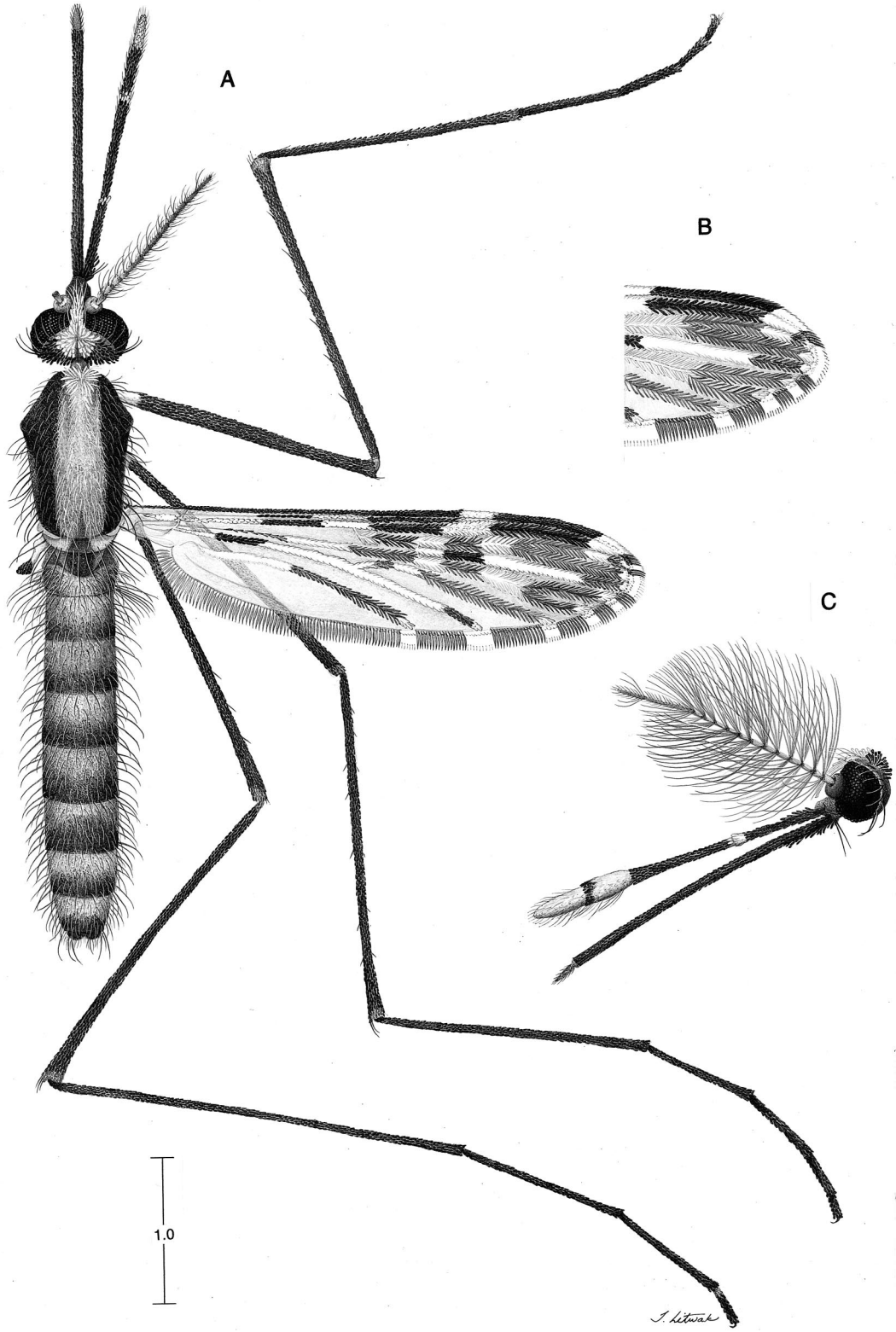

Fig. 1. *An. pseudopunctipennis*, adult. (A) Female habitus. (B) Female wing, part. (C) Male head. Scale in mm.

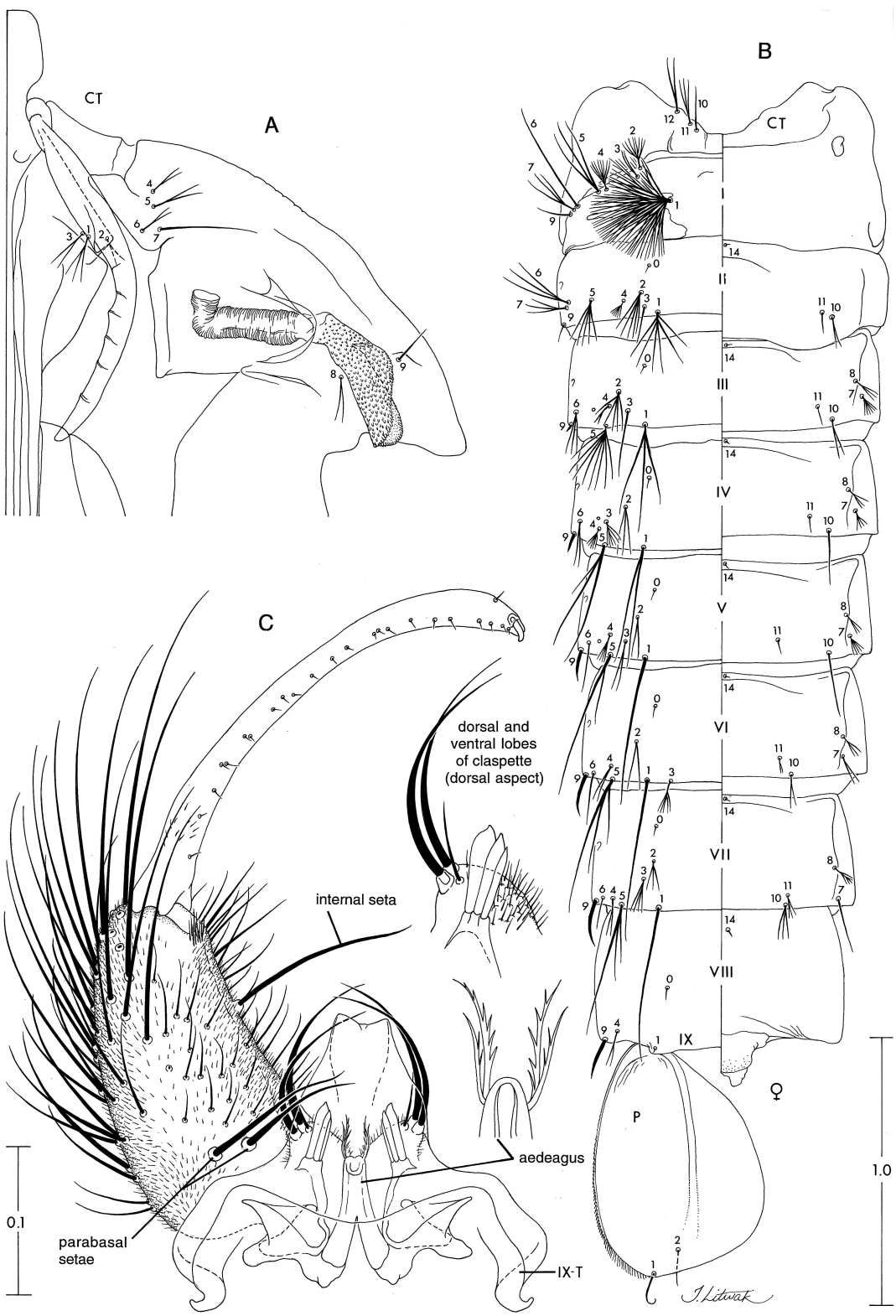

Fig. 2. *An. pseudopunctipennis.* (A) Pupa cephalothorax. (B) Pupa metathorax and abdomen, left side dorsal, right side ventral. (C) Male genitalia. Scale in mm.

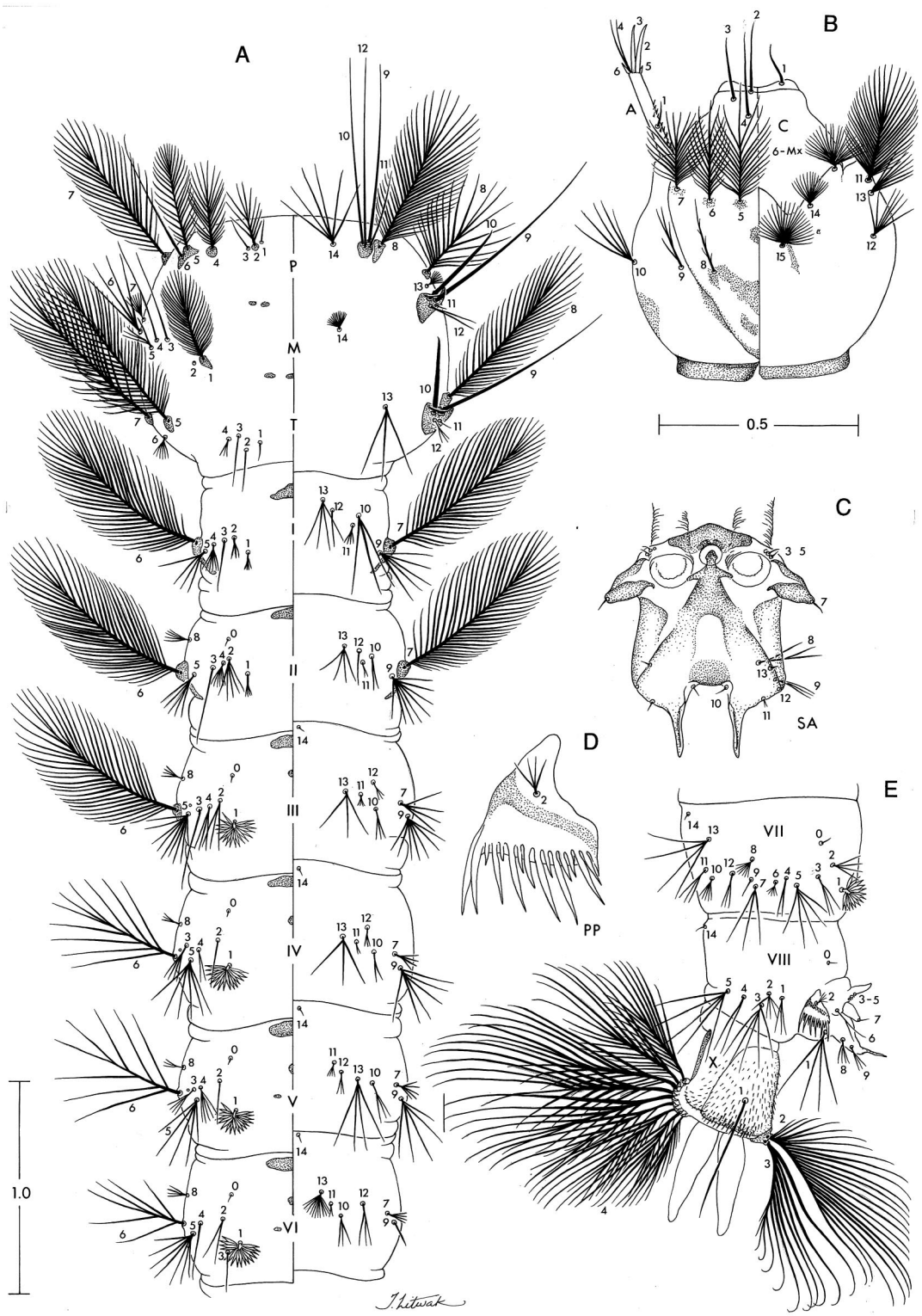

Fig. 3. *An. pseudopunctipennis*, larva. (A) Thorax and abdominal segments I–VI, left side dorsal, right side ventral. (B) Head, left side dorsal, right side ventral. (C) Spiracular apparatus, dorsal aspect. (D) Pecten and pecten teeth. (E) Abdominal segments VIII–X, side view. Scale in mm.

with two small black patches, branches of the fork-cell all dark scaled; fifth long vein with a black spot near the base, rest mostly yellow, upper branch of the fork mostly dark, a small yellow spot at the apex and another toward its base, lower branch mostly yellowish, with a black apical spot; sixth vein with basal half creamy, the apical half dark, except a small yellow patch where it joins the wing border; fringe brown, with a yellow spot at the junction of each vein. Length – 5 mm. *Male.* Last two joints of the palpi swollen and clavate, pale, basal joints dark brown, densely scaled with deep brown scales, with a narrow pale band, not quite as long as the thin proboscis, which is brown, with yellow labelae; antennae gray, with narrow brown bands and flaxen brown hairs, apical joint about half length of the joint; basal lobe of the genitalia simple, claspers long and thin; fore ungues unequal, the larger one uniserrated, the smaller minute and simple; mid and hind ungues small, equal and simple. Wings much as in the female, but the fork-cells shorter. Length – 5 mm, with proboscis 7.5 mm."

Supplemental Description

Below are additional characters of value in defining this species.

Female (Fig. 1A–B). Integument light to dark brown with silvery or grayish pollinosity. *Head.* Interocular space with 7–10 (n = 12 for this and the following measurements and counts except where indicated) long, pale setae and intermixed of long and small, narrow, appressed white scales; vertex, occiput and upper portion of postgena with numerous erect, truncate scales; patch of white scales on the middle portion of vertex; patch of dark brown to black scales on lateral portion of vertex, occiput and upper portion of postgena; long dark brown to black setae on ventral portion of postgena. Clypeus bare. Pedicel of antenna with 7–23 (n = 16) small, dorsolateral, narrow to broad, grayish white spatulate scales; flagellomere 1 with numerous narrow to broad white spatulate scales. Scales of maxillary palpus slender, spatulate mostly dark brown to black with intermixed dark brown setae; narrow band of white scales at base of palpomere 3, and at base and apex of palpomere 4; palpomere 5 mostly white scaled; base of maxillary palpus with long, erect dark setae; length of maxillary palpus 1.59–2.3 mm (mean = 1.78 mm, n = 22); ratio of length of palpomeres 2–5 to total length of palpus, 2 = 0.20–0.33 (mean = 0.26, n = 22), 3 = 0.32–0.41 (mean = 0.37, n = 22), 4 = 0.15–0.22 (mean = 0.18, n = 22), 5 = 0.08–0.13 (mean = 0.11, n = 22); ratio of palpomeres 2–5, 0.86–0.96 (mean = 0.92, n = 22); ratio of palpomeres 4–5, 0.26–0.31 (mean = 0.29, n = 22); palpus 0.62–1.18 (mean = 0.99, n = 22) forefemur length. Proboscis dark scaled, base with long, erect setae and scales; proboscis length 1.71–2.10 mm (mean = 1.86 mm, n = 22); proboscis 0.97–1.13 (mean = 1.04, n = 22) palpus length. *Thorax.* Scutal integument dark brown with a broad, median longitudinal pale frosty pruinose stripe; median stripe with narrow pale yellow scales and setae; median anterior promontory with patch of intermixed pale yellow, narrow, short and long scales. Darker lateral portions of scutum with longer dark setae. Scutal fossa, antealar area and supraalar area slightly pale dusted. Scutellum dark, slightly pale dusted with 11–24 shorter and 13–24 long setae, short setae intermixed pale yellow and dark brown, long setae dark brown. Antepronotum with 14–21 dark brown setae. Pleuron brown to dark brown; upper proepisternum with 2–7 setae, without scales; prespiracular area with 1–4 setae, without scales; prealar area with 4–10 setae; without scales; upper mesokatepisternum with 1–5 setae, without scales; lower mesokatepisternum with 1–4 setae, without scales; upper mesepimeron with 5–9 setae, rarely one fusiform white scale. *Legs.* Coxae and trochanters light to dark yellow with pale to brown setae; hindcoxae usually with two short, fusiform, dark scales; anterior surface of trochanter with light yellow scales; femora, tibiae and tarsi dark; apices of femora and tibiae with spots of pale scales. Forefemur length 1.56–2.73 mm (mean = 1.84 mm, n = 24), ratio of forefemur length to proboscis length 0.77–1.53 (mean = 0.97). *Wing* (Table 1). Length (measured from humeral cross vein) 2.76–3.21 mm (mean = 2.99 mm). Dark scales brown to black, pale wing scales white and pale yellow. Vein C dark scaled from basal to sectoral area; base of R_s white scaled; R_{4+5} with two dark spots; vein M mostly white scaled. Anal vein (1A) with pale spots at base and apex and dark spot (0.5 vein length) at distal half before apex. Pale wing fringe spots present at the distal end of each vein. *Halter.* Scabellum and pedicel with pale to pale brown integument; dorsal surface of pedicel with few pale scales at apex; capitellum dark brown to black. *Abdomen.* Integument dark brown to black with some grayish pollinosity. Terga and sterna covered with pale brown to golden brown setae.

Male (Fig. 1C, 2C). As in female except for the following sexual differences. Maxillary palpus 0.83–1.01 length of proboscis (mean = 0.91; n = 12 for this and following measurements except where indicated), apex of palpomere 3 and all palpomere 4 and 5 enlarged. Maxillary palpus (Fig. 1C) with dark brown and pale yellow scales; palpomere 2 with slightly erect dark scales at base and few pale yellow scales at apex; palpomere 3 dark scaled with pale yellow scales at base and some pale yellow setae at apex; palpomere 4 pale yellow scaled, inner surface with yellowish long setae, and base and apex with few dark scales; palpomere 5 usually totally pale yellow with numerous yellowish short setae and few dark short setae, sometimes with few dark scales on lateral surface. Proboscis length 1.68–2.46 mm (mean = 1.95 mm), dark brown scales; labela dark brown. Foreungues with slightly curved submedian tooth and blunt, external basal tooth. Ninth tergal lobe (Fig. 2C) stout, about as long as wide. Gonocoxite 1.08–1.83 times as long as wide; dorsal (postrotational) surface with shorter and long setae, very long setae distally and numerous very small spicules; most mesal parabasal spines (parabasal 1) stout with slightly recurved tip, borne on slightly raised base; parabasal 2 longer and

Table 1. ***An. pseudopunctipennis:*** **descriptive statistics for ratios of veins C and R-R_1 wing spot lengths/length of wing measured from humeral crossvein[a]**

Wing spot	Range	Mean ± SD
Vein C		
Basal dark to sector dark (BD+PHD+HD+PD+SD)	0.57–0.79	0.69 ± 0.06 [0.75]
Subcostal pale (SCP)	0.07–0.10	0.09 ± 0.01 [0.08]
Preapical dark (PD)	0.19–0.25	0.22 ± 0.02 [0.20]
Preapical pale (PP)	0.05–0.10	0.07 ± 0.01 [0.10]
Apical dark (AD)	0.02–0.03	0.03 ± 0.01 [0.03]
Vein R-R_1		
Presector dark (PSD)	0.10–0.17	0.13 ± 0.02 [0.14]
Sector pale (SP)	0.08–0.13	0.11 ± 0.01 [0.11]
Sector dark (SD)	0.16–0.23	0.19 ± 0.02 [0.20]
Subcostal pale (SCP)	0.07–0.11	0.08 ± 0.02 [0.07]
Preapical dark (PD)	0.15–0.25	0.21 ± 0.03 [0.15]
Preapical pale (PP)	0.02–0.09	0.06 ± 0.02 [0.09]
Apical dark (AD)	0.02–0.03	0.03 ± 0.00 [0.02]

[a] Fourteen wings from the neotype and alloneotype, and 12 individuals; male neotype is shown in brackets.

more slender than 1; parabasal 1 base 0.24–0.36 from base of gonocoxite; parabasal 2 base 0.20–0.33 from base of gonocoxite; internal setae slender, longer than parabasal 1, base 0.51–0.72 distance from base of gonocoxite. *Claspette.* Dorsal lobe of claspette (Fig. 2C) with three overlapping bladelike apical filaments, and ventral lobe with two long slender apical setae and a short weak subapical seta; remainder of ventral lobe and area between it and dorsal lobe with numerous prominent short spicules. Aedeagus cylindrical, broad and furcate at base; two pairs of aedegeal leaflets at apex; leaflets slender, slightly curved and serrated. Gonostylus 1.06–1.48 length of gonocoxite; many minute setae on dorsal side of gonostylus; gonostylar claw short and blunt. The descriptive statistics for ratios of male neotype costal and subcostal wing spot lengths/length of wing measured from humeral crossvein are shown in brackets in Table 1.

Pupa (Fig. 2A–B). Position and development of setae as figured; range and modal number of branches, and number of branches of male neotype shown in Table 2. Exuviae colorless to light brown. *Cephalothorax.* Trumpet simple with deep meatal cleft; length 0.44–0.56 mm (mean = 0.51 mm, n = 24 for this and the following measurements and counts except where indicated), width 0.11–0.16 mm (mean = 0.13 mm, measured at base of pinna), index 2.99–4.24 (mean = 3.85); pinna evenly rounded distally. *Abdomen.* Seta 6-I simple, slender; 7-I with 1–5 branches; 9-I simple, slender, shorter than 6-I. Seta 1-II-VII well developed; 8-II absent; 9-II simple, slender; 9-III short, pointed 0.41–1.00 (mean = 0.68) length of 9-II; 9-IV strong, pointed, 0.94–2.12 (mean = 1.54) length of 9-III; 9-V-VIII long, pointed, spine-like; 9-V 1.37–2.88 (mean = 1.90) length of 9-IV; 9-VI 0.97–1.52 (mean = 1.19) length of 9-V; 9-VII 1.00–1.43 (mean = 1.22) length of 9-VI; 9-VIII 0.69–1.69 (mean = 0.99) length of 9-VII; 9-VI 0.23–0.42 (mean = 0.37) length of segment VI; 9-VII 0.35–0.60 (mean = 0.44) length of segment VII; 9-VIII 0.30–0.65 (mean = 0.39) length of segment VIII. Segment VII 0.76–1.11 (mean = 1.01) length of

Table 2. Pupal setal branching for *An. pseudopunctipennis:* range mode (in parentheses) based on counts made on 14–26 setae of the neotype, alloneotype, and 24 specimens collected with them; male neotype is shown in brackets

Seta no.	Cephalothorax CT	Abdominal segments I	II	III	IV	V	VI	VII	VIII	IX	Paddle Pa
0	–	–	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	–	–
1	1–3 (1) [1]	10–20 (12) [18, 20]	3–6 (4) [4]	2–4 (3) [2, 3]	1–3 (2) [2, 3]	1 [1]	1–2 (1) [1]	1 [1]	1 [1]	1 [1]	1 [1]
2	1–2 (1) [1]	1–7 (5) [6, 5]	3–6 (5) [5]	2–6 (5) [6, 5]	2–3 (2) [3]	1–3 (2) [3, 2]	1–3 (1) [3]	2–4 (3) [3]	–	–	1 [1]
3	1–3 (1) [1, 2]	1–5 (3) [2, 1]	1–2 (1) [1]	1 [1]	1–7 (6) [6, 7]	1–5 (2) [4, 3]	2–5 (2) [4]	1–4 (3) [3]	–	–	–
4	1–2 (1) [1]	3–10 (5) [7]	1–8 (1) [8]	1–3 (1) [2]	1–5 (1) [2, 5]	1–5 (3) [3]	1–2 (2) [1, 2]	1–4 (2) [2, 1]	1–3 (2) [3]	–	–
5	1–3 (1) [1]	1–3 (2) [2, 3]	3–7 (5) [6, 5]	3–11 (6) [7, 5]	2–4 (3) [2, 3]	1–3 (2) [2]	1–3 (2) [3]	1–3 (2) [2]	–	–	–
6	1–2 (1) [1, 2]	1 [1]	1–2 (1) [1, 2]	1–4 (3) [3]	1–2 (1) [1]	1–2 (1) [1]	1–2 (1) [1]	1–2 (1) [1]	–	–	–
7	1 [1]	1–5 (1) [–]	1–4 (2) [2, 3]	1–6 (3) [6, 4]	1–7 (3) [3]	1–5 (3) [4, 3]	1–3 (2) [3]	1 [1]	–	–	–
8	1–3 (2) [2]	–	–	1–4 (3) [4]	1–4 (3) [3]	2–4 (3) [3, 2]	2–3 (3) [3, 2]	3–5 (3) [3]	–	–	–
9	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	–	–
10	1–2 (1) [2, 1]	–	1–2 (1) [1]	1–2 (1) [2]	1 [1]	1–2 (1) [1]	1–3 (2) [2, 1]	1–4 (2) [2]	–	–	–
11	1–4 (1) [4, 1]	–	1–2 (1) [1]	1–3 (1) [1]	1 [1]	1 [1]	1–3 (1) [2]	1–3 (3) [3]	–	–	–
12	1–3 (2) [3, 1]	–	–	–	–	–	–	–	–	–	–
13	–	–	–	–	–	–	–	–	–	–	–
14	–	–	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	–	–

Table 3. Larval setal branching for *An. pseudopunctipennis:* range mode (in parentheses) based on counts made on 12–22 setae of the neotype and alloneotype, and 20 specimens collected with them; male neotype is shown in brackets

Seta no.	Head	Thorax			Abdominal segments		
	C	P	M	T	I	II	III
0	–	–	–	–	–	1 [1]	1 [1]
1	1 [1]	1–2 (1)	28–44 (36)	1 [1]	2–4 (2) [4]	1–6 (2) [5]	10–17 (15) [16, 17]
2	1 [1]	5–11 (8) [5]	1	1 [1]	2–4 (3) [2, 3]	3–6 (5) [5, 4]	2–4 (3) [4]
3	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]
4	1 [1]	12–19 (12) [18]	1 [1]	2–3 (3) [2]	4–5 (5) [5]	3–6 (6) [5, 6]	2–6 (3) [3]
5	16–23 (20) [22]	17–28 (24) [21]	2–4 (4) [4]	21–58 (44) [49]	3–8 (5) [5]	5–7 (7) [5, 7]	4–9 (7) [5]
6	15–18 (16) [18]	1 [1]	3–5 (4) [3]	2–6 (3) [5]	35–53 (38) [41, 36]	41–49 (49) [49]	35–49 (41) [37, 41]
7	16–26 (25) [24, 25]	15–30 (15) [30]	5–8 (7) [8]	30–53 (38) [–]	32–46 (42) [45, 42]	42–48 (44) [43, 48]	2–5 (3) [2, 3]
8	3–6 (4) [3, 4]	26–44 (44) [35, 39]	10–15 (12) [15]	36–58 (42) [42]	–	2–4 (3) [2]	2–4 (3) [2, 4]
9	3–8 (4) [4]	1 [1]	1 [1]	1 [1]	4–6 (4) [4]	5–9 (8) [5, 2]	3–7 (7) [4, 7]
10	2–5 (4) [4, 2]	1 [1]	1 [–]	1 [1]	2–5 (3) [3]	2–3 (2) [2, 3]	1–3 (1) [2, 3]
11	23–37 (31) [35, 27]	1 [1]	1 [1]	1 [1]	2–5 (3) [5]	2–4 (2) [4]	2–3 (3) [2, 3]
12	3–7 (6) [4, 6]	1 [1]	2–3 (2) [2]	1–3 (1) [1]	1–3 (1) [1]	1–3 (1) [1, 3]	1–4 (2) [4, 1]
13	1–7 (1) [7]	–	9–13 (12) [9]	2–3 (2) [2]	2–3 (3) [3]	3–5 (3) [3]	3–4 (3) [3]
14	10–18 (16) [17, 15]	5–8 (7) [6]	8–20 (8) [8]	–	–	–	1 [1]
15	13–22 (16) [13]	–	–	–	–	–	–

Seta no.	Abdominal segments					
	IV	V	VI	VII	VIII	X
0	1 [1]	1 [1]	1 [1]	1 [1]	1 [1]	–
1	14–18 (16) [17, 18]	14–18 (16) [15, 14]	13–18 (16) [17, 18]	14–16 (15) [15, 14]	1–3 (3) [2, 3]	1 [1]
2	1 [1]	1 [1]	1–2 (2) [2]	2–4 (4) [4]	3–5 (5) [5]	16–51 (18) [19]
3	1–4 (4) [4]	3–4 (3) [3]	1 [1]	2–3 (3) [3]	4–6 (5) [4, 5]	6–22 (6) [12]
4	2–4 (2) [2]	3–5 (5) [4, 5]	1 [1]	1–2 (2) [2]	1–3 (1) [3, 2]	9 [9]
5	3–6 (5) [5]	3–6 (4) [4, 6]	4–7 (5) [5]	4–5 (5) [4]	2–5 (4) [4, 5]	–
6	5–10 (8) [10, 9]	5–8 (5) [7, 8]	4–7 (6) [4, 5]	3–6 (3) [6]	1-S	2–6 (4) [2]
7	2–4 (3) [3]	2–5 (3) [4, 3]	3–4 (3) [3]	2–4 (3) [3]	2-S	3–5 (4) [–]
8	2–4 (2) [4, 3]	3–4 (3) [3]	3–4 (3) [–]	3–8 (7) [3]	6-S	1–2 (2) [2]
9	3–6 (5) [4, 5]	3–5 (5) [5, 4]	1 [1]	1 [1]	7-S	1 [1]
10	1–3 (2) [1, 2]	1–5 (3) [3]	2–4 (3) [4]	3–5 (5) [3]	8-S	3–5 (3) [5]
11	1–4 (2) [4, 1]	2–4 (3) [3]	1–4 (2) [4]	1–3 (2) [1]	9-S	2–4 (3) [3]
12	1–3 (1) [1, 3]	1–3 (2) [3]	1–3 (3) [1]	2–3 (3) [3]	–	–
13	3 [3]	3–5 (3) [5, 4]	8–13 (12) [13]	3–6 (4) [3]	–	–
14	1 [1]	1 [1]	1 [1]	1 [1]	1–3 (1) [3]	–
15	–	–	–	–	–	–

C, head; P, prothorax; M, mesothorax; T, metathorax.

segment VI; segment VIII 1.00–1.24 (mean = 1.11) length of segment VI; segment VIII 1.00–1.63 (mean = 1.12) length of segment VII. Segment VII 0.76–1.11 (mean = 1.01) width of segment VI (width at posterior margins); segment VIII 1.00–1.24 (mean = 1.12) width of segment VI; segment VIII 1.00–1.63 (mean = 1.12) width of segment VII. Width/length of segment VI 1.94–2.71 (mean = 2.36), VII 1.79–3.30 (mean = 2.22), VIII 1.67–2.02 (mean = 1.89). Paddle length 0.74–0.96 mm (mean = 0.87 mm, n = 13), width 0.54–0.69 mm (mean = 0.61 mm, n = 13), length/width ratio 1.32–1.56 (mean = 1.44, n = 13) somewhat oval; refractile index 0.82–0.94 (mean = 0.90, n = 13); length of marginal spicules 0.01–0.04 mm (mean = 0.02 mm, n = 13).

Larva (Fig. 3). Position and development of setae as figured; range and modal number of branches and number of branches of male neotype as shown in Table 3. *Head.* Lightly pigmented, particularly in the middle part; length 0.80–0.94 mm (mean = 0.87 mm, n = 11), width 0.56–0.78 mm (mean 0.72 mm, n = 11). Antennal length 0.24–0.30 mm (mean = 0.27 mm, n = 12), slightly tapered toward apex, 5.67–8.67 (mean = 6.76, n = 12) longer than wide; with 11–19 (mode = 14, n = 18) spicules on mesal and ventral surfaces; spicule length 0.01–0.02 mm (mean = 0.01 mm, n = 23). Seta 1-A single, slender, 0.04–0.08 mm (mean = 0.07 mm, n = 12), inserted 0.34–0.42 (mean = 0.37) from base of antenna; 2,3-A single, pointed; 4-A with 2–5 branches (mode = 3, n = 13); 5-A short, spine-like, 0.15–0.60 (mean = 0.32, n = 12) length of seta 1-A; 6-A spine-like ≈2–3 times longer than seta 5-A. Seta 2-C single 1.00–1.53 (mean = 1.27, n = 12) length of 3-C; seta 2-C almost close to mate of opposite side 0.02–0.03 mm (mean = 0.03 mm, n = 11); 3-C single, 0.66–1.00 (mean = 0.80, n = 12) length of 2-C, clypeal index (distance between bases 2-C and 3-C on one side/distance between bases of 2-C) 1.75–3.00 (mean = 3.07, n = 12). *Thorax.* Seta 1-P single or double; 9–12-P single; 9–12-P setal support plate spine length 0.05 mm. Seta 9–11-M single; 9-M 2.00–2.20 (mean = 2.09, n = 7) length 10-M; seta 12-M with 2–3 branches; 9–12-M setal support plate spine length 0.08–0.13 mm (mean = 0.10 mm, n = 13). Seta 9–11-T single; 9-T 2.02–2.40 (mean = 2.17, n = 10) length of 10-T; seta 12-T with 1–3 branches; 9–12-T setal support plate spine length 0.08–0.13 mm (mean = 0.09 mm, n = 12); 13-T with 2–3 branches. *Abdomen.* Seta 1-I with 2–4 branches (mode 2, n = 12); 1-II single or with 2–6 branches (mode = 2, n = 12) arising on the distal half.

Seta 1-III-VII palmate with well developed leaflets, each leaflet with short filament; 0-II-VIII, 14-III-VIII weakly developed; 0, 8, 14-I, 14-II absent or rare; 3-I-III, VI single; 3-IV, V, VII, VIII branched; 6-II-VII branched. Anterior tergal plates on segments III-VIII small, ≈0.20 width of the segment, not enclosing small median posterior plate. Seta 1-X single, long, 0.92–1.67 (mean = 1.27, n = 11) length of saddle; 1-X inserted on saddle. Saddle with minute, sparse spicules on lateral surface. Integument of posterior margin of segment X with strongly developed, dark spicules. Setae 2–3-X with hook-like tips that are used to hold the larvae on substrate in a water current. *Spiracular apparatus.* Pecten plate with 12–18 spines; arrangement of spines alternating long and short, with 5–10 (mode = 7, n = 20) long spines and 4–9 (mode = 7, n = 20) short spines; long spines 1.67–5.40 (mean = 2.92, n = 38) length of short spines. Two posterolateral spiracular lobe plates each with elongate, slender, sclerotized projection or "tail" from inner caudal margin. Table 3 also shows the range and modal number of branches of siphon setae (1, 2, 6–9-S).

Type Material. Neotype: Male with associated slide mounted larval and pupal exuviae and slide mounted genitalia, from the progeny brood of a female captured on human bait, data as follows: Grenada, Rio Sallee, Chambord Estate, S. Manguin, and E. L. Peyton Coll. 13 April 1992, 12° 12′ N, 61° 37′W, collection and specimen no. GR 30(1)-2. Deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. (WRBU ACC No. 1539/WRBU/USUHS). Alloneotype: Female with associated slide mounted larval and pupal exuviae, collection and specimen no. GR 30(1)-3, with same collection data as male neotype.

Other Material Examined. A total of 182 specimens in the National Museum of Natural History, Smithsonian Institution, Washington, DC, consisting of 50 females, 36 males, 48 pupal exuviae, 27 larval exuviae, 14 larvae, and 7 male genitalia.

Grenada. Rio Sallee, St. Patrick, E. L. Peyton coll., 13 April 1992, 12° 12′ N, 61° 37′W. GR 29–23 M PeLe; GR 29–33 M; GR 29–36 M; GR 29–37 F; GR 29–108 M; GR 30(1)-1 M PeLe; GR 30(1)-100 M Pe; GR 30(1)-101 F Pe; GR 30(1)-102–103 M Pe; GR 31 L; GR 31–3 PeLe; GR 31–17 F; GR 31–35-38 F; GR 31–113 M Pe; GR 31–114 Pe; GR 31–115 Pe; GR 31–116 F Pe; GR 31–117-120 M Pe; GR 31–121-129 Pe; GR 31–131 F Pe; GR 31–132 Pe; GR 31–134-135 M Pe; GR 31–137 Pe; GR 31–138 M Pe; GR 31–137 M; GR 31–141 M Pe; GR 31–142-144 Pe; GR 31–145-149 M Pe; GR 33 L; GR 33(1) L; GR 33–1 PeLe; GR 33–2-6 F PeLe; GR 33–7 PeLe; GR 33–8 F; GR 33–9 F PeLe; GR 33–10 F; GR 33–11-12 M PeLe; GR 33–13-15 PeLe; GR 33–17-19 PeLe; GR 33–20 M PeLe; GR 33–21-24 F PeLe; GR 33–25-26 F; GR 33–27 PeLe; GR 33–28 F PeLe; GR 33–100-118 Pe; GR 33–117 M; GR 33–119 M; GR 33–121-128 F; GR 33–129-130 M; GR 33–132-134 F; GR 33–133-134 F; GR 33–135-136 M; GR 33–137-139 F; GR 33–140 M; GR 33–142 F; GR 33–143 M; GR 33–145 F; GR 33–146 M; GR 33–147-153 F; GR 33–154 M; GR 33–155-156 F; GR 33–158-160 M. Soubise River, St. Andrew, W. A. Hoffman coll., 26 August 1929, LAR 41, 710106–3, 4, 5, 6 G; LAR 41, 710201–1 G; Chambord Mineral Spring, St. Patrick, LAR 48, 710201–4 G; R. Martinez, coll., 28 October 1963, Queens Park Oval, St. George, GR 90, 710106–3 G.

Distribution. Argentina, Belize, Bolivia, Chile, Colombia, Costa Rica, Ecuador, El Salvador, Grenada, Guatemala, Haiti, Honduras, Mexico, Nicaragua, Panama, Peru, Trinidad and Tobago, United States, Venezuela.

Medical Importance. Through out its range, *An. pseudopunctipennis* is generally the most important vector of malaria in mountainous areas during the dry season (Shannon et al. 1927, Aitken 1945, Rodriguez and Loyola 1989). It transmits malaria in highly elevated areas up to 2,800 m in Bolivia (Hackett 1945, Gorham et al. 1973). It is also the dominant malaria vector in seven of 19 (37%) countries with endemic malaria (Pan American Health Organization 1994), including Argentina, Bolivia, Ecuador, Guatemala, Mexico, Nicaragua, and Peru (Manguin et al. 1996).

Bionomics. The larvae of *An. pseudopunctipennis* are found in a variety of habitats but they occur frequently in sun-exposed freshwater stream pools containing filamentous green algae (e.g., *Spirogyra*, *Oedogonium*, *Cladophora*, *Closterium*, *Enteromorpha*) and aquatic vegetation with clear, shallow, and stagnant water (Manguin et al. 1996). The green algae provide oviposition substrates for gravid adult females as well as food and shelter for the mosquito larvae. Larval habitats are common in dry environments in valleys and foothills. Larvae are tolerant of water temperature fluctuations and drought. This species is most abundant during the dry season. Larval abundance is usually negatively associated with seasonal rainfall. Heavy rains cause rivers and tributaries to rise suddenly and transform into rapidly flowing waters. As a consequence, typical oviposition and larval breeding sites such as flood-plain pools, stream margins, and ditches are destroyed by excessive flooding. Alternative larval habitats include spring-seepages, ground pools, lagoons, rock pools, artificial containers (e.g., reservoirs, tanks, fountains, well holes), rice paddies, and marshy meadows. Larvae are found in habitats with acidic, neutral and alkaline water (pH 4.5–8.8), freshwater to brackish water (conductivities from below 650 up to 8,350 uS), at elevations as low as sea level up to 3,200 m. Adult females are highly anthropophilic and they enter houses readily for shelter. The indoor resting females usually attack humans. They also feed freely outdoors on humans, cattle, horses, and other animals.

Discussion

Although Theobald (1901) provided the original description of *An. pseudopunctipennis*, it was not sufficient for accurate identification of the species. This resulted in confusions and misidentifications of the species in many parts of its geographical range in North, Central, and South America (Manguin et al.

1993). The morphological information in this paper may help in solving those problems.

Anopheles pseudopunctipennis has the following diagnostic features. *Adult female:* Maxillary palpus has palpomere 5 mostly white scaled; base of wing vein Rs white scaled; vein M predominantly pale scaled. *Adult male:* The male terminalia has dorsal lobe of claspette with three overlapping bladelike apical filaments. Aedeagus is cylindrical, broad and furcate at base; two pairs of aedegeal leaflets at apex; leaflets slender, slightly curved, and serrated. *Larva:* The spiracular apparatus has two posterolateral spiracular lobe plates each with elongate, slender, sclerotized projection or "tail" from inner caudal margin. Seta 2-IV single; 3-C single; 9-M and 9-T about twice the length of 10-M and 10-T. Detailed comparisons of pupal characters of *An. pseudopunctipennis* and related species are needed to further clarify species differences. Other morphological features described in this paper for larva, pupa, and adults may be used to separate *An. pseudopunctipennis* from related species.

The status of *An. pseudopunctipennis* as a single species or a species complex is controversial and confusing (Estrada-Franco et al. 1992, 1993a, 1993b; Manguin et al. 1995; Munstermann 1995; Coetzee et al. 1999). Manguin et al. (1995) conducted a comprehensive electrophoretic survey of 42 populations of this species collected from 10 countries in North, Central, and South America throughout its geographic distribution. They found no fixed electromorphic differences separating the populations of the species. Based on the isoenzme analyses, however, they found three geographic populations of *An. pseudopunctipennis,* with Grenada (type-locality) populations as a distinct one. Estrada-Franco et al. (1992, 1993a, 1993b) found genetic differences among geographic strains of *An. punctipennis* in neotropical America, and they suggested the presence of at least allopatric sibling species in the region. Coetzee et al. (1999) suggested a third species of *An. pseudopunctipennis* complex based on cytogenetic tests of mosquito populations from Mexico and Grenada.

With the designation of neotype and detailed descriptions of various life stages of *An. pseudopunctipennis,* future studies may be conducted using various tools, including morphological, molecular, or biochemical, to solve the complexity of this widespread species. Because of its major involvement in malaria transmission, there is an urgent need to clarify the taxonomy of *An. pseudopunctipennis* complex, if multiple species exist, through comparisons of various populations of mosquitoes from different countries of North, Central and South America.

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